Title: **Social instability raises the stakes during social grooming among wild male chimpanzees**

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Summary

Explaining cooperative behaviour is fundamental issue for evolutionary biology. The problem any cooperative strategy faces is minimizing risks of non-reciprocation (cheating) in interactions with immediate costs and delayed benefits. One of a variety of proposed strategies, the raise-the-stakes (RTS) strategy posits that individuals establish cooperation by increasing investment across interactions from an initial interaction. This model has received little quantitative support, however, probably because individuals of many social species engage in repeated interactions from a young age. In some situations, however, such as following conflicts, after prolonged absences, or during social instability, established relationships may become unreliable predictors of future behaviour, create an environment for RTS. We investigated grooming interactions among wild male chimpanzees (*Pan troglodytes*), testing RTS in these specific contexts. We found evidence that male chimpanzees employed RTS during social instability, but not under the other conditions. However, this patterning of grooming interactions was, we suggest, less to do with preventing cheating and more to do with avoiding the elevated risks of intra-male aggression during the period of social instability: social instability raises the stakes for grooming by creating a more hazardous marketplace in which to trade.

Introduction

Explaining cooperative behaviour is a fundamental question for evolutionary biology (West et al. 2006). While cooperation between related individuals is often accounted for by indirect benefits and inclusive fitness theory (Hamilton 1964a, b), cooperation between unrelated individuals is typically explained by invoking the theory of reciprocal altruism (Trivers, 1971) with its exchange of direct costs and benefits, albeit delayed in time. Functionally, this is mutualism rather than altruism as all actors receive direct fitness benefits and is better described as direct reciprocity (Clutton-Brock 2009).

The problem faced for any cooperative strategy is how to minimize risks of non-reciprocation (cheating) in interactions in which costs are immediate but benefits are delayed. A variety of strategies have been proposed, building on the iterated prisoner's dilemma (IPD) model suggested by Trivers (1971). Axelrod and Hamilton's (1981) 'tit-for-tat' strategy (TfT), under which individuals start out cooperating and match their opponent's behaviour in previous interactions, refusing to cooperate only if the partner does so first, is evolutionarily stable. TfT has found some support but seems restricted to simple social exchanges (e.g. serranid coral-reef hermaphroditic fish: Fischer, 1988), or artificial experimental situations (e.g. predator inspection by sticklebacks and guppies: Milinski 1987; Dugatkin 1988). Strategies based on an IPD model assume cooperation to be an 'all-or-nothing' affair, and that interacting individuals have no other potential social partners (Noë 1990, 2001); in consequence, a variety of further models with more applicability to biological systems have been proposed, such as Biological Markets theory (Noë 2001, 2006; Noë and

72 Hammerstein 1994, 1995), pseudo-reciprocity (Connor 1986), parcelling (Connor
73 1992) and raise-the-stakes (Roberts and Sherratt 1998; Sherratt and Roberts 2002).
74
75 Raise-the-stakes (RTS) describes a strategy in which co-operators increase
76 investment in a social interaction if the partner matches or betters their opponent's last
77 move. It allows cooperation to be incremental, rather than 'all-or-nothing', and
78 individuals' investment in a relationship can vary over a series of interactions
79 (Roberts and Sherratt 1998; Sherratt and Roberts 1999). RTS allows the animals to
80 'test the water', before investing in potentially costly cooperative behaviours; at the
81 very least, it allows them to limit their losses. This strategy is robust against 'subtle
82 cheaters': individuals that invest less than in previous interactions (Roberts & Sherratt
83 1998; Van den Berg and De Witte 2006) and generates predictions that can be easily
84 tested in animal systems (Keller and Reeve 1998). Support for RTS has been found in
85 species as diverse as the sawfly *Perga affinis*, where cohesion among gregarious larva
86 is maintained through tapping signals and the group's investment (Fletcher 2008), and
87 humans *Homo sapiens*, where subjects increased monetary donations to a social
88 partner if that partner matched their investment (Roberts and Renwick 2003; Majolo
89 et al. 2006; Van den Berg and De Witte 2006) but not where the partner was a
90 previously established friend (Majolo et al. 2006; Krebs 1970).
91
92 The initial presentation of the RTS strategy was supported by data on
93 grooming reciprocity in impala *Aepyceros melampus* (Roberts and Sherratt 1998) and
94 social grooming should be an ideal behaviour with which to test the usefulness of
95 RTS as an explanation for reciprocity: the total amount of grooming that one
96 individual performs for another is easily broken down into smaller 'episodes' of

investment, and that investment can be quantified by time spent giving grooming (Roberts and Sherratt 1998; Keller and Reeve 1998). Grooming offers benefits to the recipient, in terms of ectoparasite removal (Mooring et al. 2004) and stress reduction (Aureli et al. 1999; Gust et al. 1993; Kaburu et al. 2012) at some costs to the groomer, such as reduced vigilance (Maestripieri 1993; Cords 1995; Mooring and Hart, 1995) and resting time (Dunbar 1992). Studies of grooming in non-human primates, suggested as an example system for RTS by Keller and Reeve (1998), have failed to find support for this strategy, however (Barrett et al. 2000; Manson et al. 2004; Fruteau et al. 2011).

RTS assumes an initial interaction from which reciprocity can develop and so appears most applicable to situations where individuals are forming new cooperative relationships (*sensu* Hinde 1976). In many animal groups, however, most observed social interactions are merely the latest of a series of interactions that may have started in infancy: the relevance of RTS for understanding persistent reciprocity between members of complex social groups has therefore been questioned (Barrett et al. 2000; Barrett and Henzi 2006). There are several possible scenarios under which this history of interactions may be negated, at least temporarily. These could include aggressive conflicts, prolonged absences from a group or periods of high social instability. If this occurs, and individuals cannot rely on their prior history of interactions to predict future behaviour, they may need to use strategies such as RTS to re-establish cooperative relationships. The impact of such contexts on grooming strategy has not been examined.

Here we examine grooming exchanges among wild male chimpanzees (*Pan troglodytes*) for evidence of the RTS strategy. The grooming behaviour of adult male chimpanzees offers a good model system for the investigation of reciprocity. Previous work has shown that chimpanzees tend to reciprocate grooming exchanges (Newton-Fisher 1997, 2002; Newton-Fisher & Lee 2011; Watts, 2000; Mitani 2006; Arnold and Whiten 2003; Gomes et al. 2009; Boesch and Boesch-Achermann, 2000). Furthermore, chimpanzees tend to break down grooming bouts into small episodes (*sensu* Barrett et al. 2000), the length of which can vary both within and across bouts. The chimpanzee social system is characterised by fluid associations, with any particular set of individuals often only stable on a timescale of minutes or hours and individuals may be out of contact with particular others for hours or days as a result (Reynolds 1965; Nishida 1968).

Given the results of previous studies of primate grooming exchanges (Barrett et al. 2000; Manson et al. 2004; Fruteau et al. 2011), we predict that RTS will not be a strategy employed during social stability (*prediction 1*). In contrast, we predict that they will adopt RTS in contexts where relationships may be 'reset': that is, where prior histories of interaction may become unreliable predictors of the behaviour of social partners, thus creating a need to re-establish grooming relationships. We focus on three specific contexts:

1. *The aftermath of aggressive conflicts*. Across a range of primate species both aggressor and victim tend to be more anxious after a conflict (reviewed in Aureli and Smuncy 2000), especially where they had previously shown a high level of affiliation (Kutsukake and Castles 2001; Aureli, 1997; Cords and Aureli 2000). Conflicts can potentially jeopardize the relationship between two individuals (Aureli and de Waal 2000; Cords and Aureli 2000; Aureli et al.

2002; Silk 2002) and former opponents may try to repair their relationships (Cords and Aureli 2000) by reconciling (de Waal and van Roosmalen 1979; Silk 2002), suggesting that they can no longer rely on prior history to guide future cooperation. Reconciliatory tendency in wild chimpanzees is relatively low, however, occurring in only 12-16% of dyads (Arnold & Whiten, 2001; Kutsukake & Castles, 2004; cf. 27-35% in captivity: de Waal & van Roosmalen; Preuschoft et al 2002), so RTS may provide an alternative strategy (*prediction 2*).

2. *After prolonged absence*. Male chimpanzees may be apart from others for many days or weeks if they pursue a consortship mating strategy, by which they isolate themselves and a single (cycling) female from the rest of the social group in an attempt to gain exclusive mating access (Tutin 1979; Goodall 1986; Nishida 1997; Matsumoto-Oda 1999). The duration of this separation, together with shifting patterns of interactions between other males, may create a context in which males re-joining the other members of the social group may be unable to rely on past history and need to employ the RTS strategy to re-establish cooperative relationships (*prediction 3*).

3. *During periods of social instability*. Loss of key individuals through predation or, particularly in chimpanzees, conspecific lethal violence (Newton-Fisher & Emery Thompson 2012), may disrupt existing patterns of social interaction and/or destabilise rank hierarchies (Wey et al. 2008; Cheney and Seyfarth 2009). During our study period, a phase of elevated aggression rates and high instability in the male hierarchy followed the killing of the incumbent alpha-

male of study community (Kaburu et al. 2013). We use this dramatic shift to examine whether male chimpanzees employ RTS in their grooming interactions in periods of high social instability (*prediction 4*).

Materials and Methods

Data collection

The study was conducted between February and November 2011 on the *M-group* chimpanzee community of the Mahale Mountains National Park, Tanzania (for descriptions of the field site see: Nishida 1990, 2012; Nakamura and Nishida 2012). The study group initially consisted of 10 adult males (≥16 yr), 5 adolescent males (9-15 yr), 2 juvenile males (5-8 yr), 3 infant males (0-4 yr), 23 adult females (≥14 yr), 7 adolescent females (7-13 yr), 5 juvenile females (3-6 yr), and 5 infant females (0-2 yr). During data collection, two females gave birth, one female joined the community, while two cycling females disappeared (and were assumed to have dispersed to another group), and one adult male, the alpha, was killed (Kaburu et al. 2013).

Eight adult males were followed through day-long focal sessions (Altmann 1974). Each day, the individual previously sampled less frequently was selected as focal animal in an effort to equalise number of hours of observation across individuals. To assure independency between the focal samples, the same animal was not followed during two subsequent days. A total of 397 hours of observation were recorded (Table 1; mean ± SD / focal male = 49 ± 5 hours).

Data concerning grooming bouts were collected using both focal animal and *ad libitum* sampling. Grooming sessions were thoroughly described by voice using a dictaphone. Specifically, the identity of the partners, the time spent giving or receiving grooming, and events when one or both the individuals stopped grooming were recorded. Bouts that were underway at the beginning of the observation period and/or whose pattern could not be accurately observed due to poor visibility were discarded. Additionally, from focal animal samples, we collected directed aggressive interactions in which an individual attacked a specific partner either by physical contact (e.g. kicking, hitting, slapping) or by chasing or agonistic displays.

Data analysis

A grooming bout was defined as a dyadic grooming interaction where one or both individuals exchanged episodes of grooming, and it was considered ended when both males engaged in other activities, including simple resting, for more than 30s (after Newton-Fisher and Lee 2011). We defined intra-bout episodes as unbroken continuous grooming given by one individual. An episode ended when neither of the groomer's hands was in contact with the recipient.

We looked for evidence of RTS both across and within grooming bouts, and tested our predictions for the absence (during social stability) and presence (in specific contexts) of the RTS strategy as detailed below. Except where indicated, all analyses were conducted using SPSS (ver. 20).

To test *prediction 1*, we analysed grooming interactions collected in the period February-September 2011, which corresponded to a period of social stability (Kaburu et al., 2013). If RTS was used as a strategy across grooming interactions, then we expected to see (a) an increase in the length of episodes across grooming bouts, as evidence of increasing investment in a cooperative relationship, and (b) the amount of grooming performed in one bout to match the amount received in the previous bout, as the strategy requires at least matching of the partner's previous investment. We used two-tailed Spearman's rank correlations to examine the relationship between length of episodes and order of occurrence, for each male's grooming history for each grooming partner. We restricted this analysis to those males recorded performing at least five episodes. To avoid pseudo-replication, the contribution of each male to each of his grooming dyads was tested individually, giving 45 possible dyads and 90 possible groomer-receiver combinations. These results were combined using a weighted Z-test (Stouffer et al. 1949; Whitlock 2005), implemented by the program MetaP (Dongliang 2009). This method is preferable to Fisher's test for combining probabilities (Sokal and Rohlf, 1981) as it is not sensitive to small (hence significant) p-values and treats large and small p-values equally: the weighted Z-test is less likely to result in a type I error (Whitlock, 2005). In order to control for the different contributions of each male to the dataset, weights were selected as the number of grooming episodes that individuals performed.

We used a Linear Mixed Model (LMM) to test whether the amount of grooming performed in one bout matched the amount received in the previous bout. LMM offers the opportunity to assess the effect of multiple independent variable(s) while controlling for repeated sampling of the same individuals (treated as random

244 factors: Pinheiro and Bates 2000). Our dependent variable was duration of grooming
245 performed, while duration of grooming received in the previous bout involving the
246 same dyad was set as an independent factor. Grooming durations were log-
247 transformed to normalise the data. We controlled for the differential contribution of
248 dyads by including dyad identity as a factor. Identities of groomer and recipient were
249 treated as random factors, while the number of grooming bouts was set as repeated
250 measurement. It was possible to conduct this type of analysis as each focal animal
251 was followed for the whole day, which offered the opportunity to identify the
252 temporal sequence of grooming interactions between each grooming pair. Grooming
253 bouts in chimpanzees can be either unidirectional (only one individual takes the role
254 of groomer) or bidirectional, with the latter involving either alternating or
255 simultaneous grooming; many bouts include a combination of these structures.
256 Unidirectional grooming is common (e.g. Newton-Fisher and Lee 2011; Gomes et al.
257 2009; see results), and we included episodes from unidirectional bouts as well as
258 those where both members of the dyad groomed as unidirectional grooming is likely
259 to play an important role in ensuring that grooming is reciprocated over time (Gomes
260 et al 2009).

261 Following Barrett et al. (2000), we tested for evidence of RTS within bouts by
262 examining whether duration of grooming episodes matched or exceeded previous
263 episodes both performed and received, for each reciprocated bout in which partners
264 alternated the roles of groomers and receivers. We assigned a plus sign when either
265 the initiator (i.e. the individual who started the bout) or the reciprocator (i.e. the
266 individual who returned the grooming) increased or matched grooming time
267 throughout the bout compared to either their own previous episodes or partner's
268 previous contribution, excluding periods of simultaneous (mutual) grooming. We

grouped bouts on the basis of the number of intra-bout episodes, and analysed only those groups where at least 5 dyads contributed data. We used two-tailed sign-test to assess whether the number of bouts in which there was a consistent increase in the duration of grooming episodes (indicated by a plus sign) significantly exceeded the number of bouts in which there was no consistent increase in grooming episode duration (indicated by a minus sign). The p-values from these multiple tests were then combined with the weighted Stouffer's Z-method. In this case weights were selected as the number of bouts that contributed to each group.

Context 1: after conflicts

Following Arnold and Whiten (2001), we defined the post-conflict context as the 30-minute period following an aggressive interaction. The window of opportunity for grooming provided by this context is short, and so we looked for evidence of RTS exclusively within bouts. We extracted grooming interactions between former opponents from post-conflict contexts and analysed bouts containing at least three episodes, as explained above.

Context 2: After prolonged absence

During the study, two adult males (*PR* & *AL*) engaged in consortship behaviour; in both cases with the same cycling female (*EF*). The consortship between *PR* and *EF* started on 7th of March. This was interrupted after 42 days (on 18th of April), but resumed on the 21st of April, lasting another month (until 24th of May). The consortship between *AL* and *EF* started on the 6th of August 2011, and lasted 52

294 days (concluding on 27th of September). We examined all grooming bouts recorded
295 within one month after each male resumed normal association with the other adult
296 males. We tested for RTS both across and within-bouts as explained above. Unlike for
297 the analysis conducted during social stability, we carried out one-tailed Spearman's
298 rank correlation tests as we predicted a positive relationship (an increase in episode
299 length across bouts).
300
301 *Context 3: Social instability*
302
303 The alpha male (*PM*) for most of our study period was killed in a coalitional
304 attack on 2nd of October, triggering a period (hereafter: the 'unstable period') of high
305 rank instability and increased aggression rates (Kaburu et al. 2013). We extracted
306 grooming data collected in this period, and compared grooming interactions with
307 those collected in the period prior to this event (hereafter: the 'stable period'). For this
308 comparison we included grooming bouts recorded both from focal and *ad libitum*
309 observations, and grooming data collected from the two non-focal males (*DW* and
310 *XM*). Across the two periods, we used Wilcoxon signed-rank tests (two-tailed) to
311 compare (a) the mean duration of grooming bouts for each dyad ($N = 35$); (b) the
312 mean episode length and the number of episodes per bout for each male ($N = 9$), and
313 (c) rates of both bouts and episodes for focal males ($N = 7$). We had previously
314 determined that rates of aggression were significantly elevated in the 'unstable period'
315 (average rate per male: 0.45 vs. 0.16 interactions/hr; $T = -2.37$, $N = 9$, $P = 0.018$:
316 Kaburu et al, 2013); to investigate whether rates of aggression changed within this
317 period, we derived daily rates of aggression by dividing the number of aggressive
318 interactions recorded during each observation day by the observation time, and used a

two-tailed Spearman's rank correlation test. Additionally, since, in chimpanzees, during social instability males are often observed disrupting grooming interactions between rivals (de Waal 1982, 1984; Nishida 2012; personal observations), we tested whether, in the period following *PM*'s death, temporal variation in episode length was predicted by aggression rates. To this end, we ran an LMM analysis in which males' daily mean grooming episode length was treated as dependent variable, while rates of aggressive interactions males participated either as aggressor or as a victim were entered as fixed factors. The ID of the males was entered as random factor and the number of days males were recorded grooming was included as repeated measure. Finally, we tested for RTS both across and within bouts, as described above.

Results

We collected 593 complete grooming bouts and 2168 grooming episodes in the stable period, corresponding to 51hr 45min of grooming time, with a mean across dyads of 13.17 bouts (± SD = ± 12.30; median = 9), and 48.18 episodes (± SD = ± 45.41; median = 38). Mean bout length was 5min 16s (± SD = ± 7 min 36s; median = 2 min 42s). Grooming rate was 1.10 bouts/hr, and 9 min 58s of grooming/hr. Mean episode length was 1min 34s (± SD = ± 1min 45s; median = 1 min, range = 1s – 20min 2s). Most bouts (69%: 412/593) were unidirectional. The majority (51%: 93/181) of bidirectional bouts were a mixture of alternating and simultaneous grooming; 29% (52/181) combined unidirectional and simultaneous grooming, while only a small proportion were exclusively alternating (15%: 27/181) or simultaneous (5%: 9/181) grooming.

Across bouts, mean episode duration tended to significantly decrease over time, with 65% of the individuals showing a negative trend (weighted Z-test: mean r_s = – 0.09, $P < 0.001$; Table 2). Additionally, the duration of grooming performed did

not match that received in the previous intra-dyadic bout (LMM: *Estimate* ± *SE* = 0.10 ± 0.07, *Wald* = 2.014, *P* = 0.158).

Within bout, groomers did not increase the length of grooming episodes in response to the duration of their own previous contribution (weighted Stouffer's Z method: N = 3, *P* = 0.97; Table 3). Additionally, the number of bouts in which individuals increased episode duration in response to the duration of partner's previous episode length was significantly lower than the number of bouts in which there was no increase of episode duration (weighted Stouffer's Z method: *N* = 2, *P* < 0.001; table 3). Therefore, male chimpanzees did not raise the stakes during social stability supporting prediction 1.

Context 1: after conflicts

Of 114 aggressive interactions involving focal individual, only 23 were followed by a grooming session between former opponents. Of these, more than half (52%: 12/23) were unidirectional, whilst the others were a combination of mutual and alternating grooming. We found no convincing evidence that males consistently increased the duration of grooming episodes during post-conflict grooming bouts either in relation to their own previous contribution or to partner's (Table 4). Our data therefore do not support prediction 2: male chimpanzees did not raise the stakes in post-conflict grooming.

Context 2: After prolonged absence

We collected 112 grooming bouts between the consorting male and the other adult males across the two post-consortship months. These bouts included 455 episodes, totalling 7hr 48min of grooming. Most groomers tended to significantly decrease episode duration over time (weighted Z-test: mean $r_s = -0.04$, $P < 0.001$; Table 2) and the amount of grooming an individual received during a bout did not significantly predict the amount of grooming he gave the partner in the subsequent bout (LMM: *Estimate* ± *SE* = 0.17 ± 0.11, *Wald* = 1.032, *P* = 0.449). Within bout, males did not show significant increase in episode duration either in relation to their own previous contribution, or to partner's (Table 5). Our data therefore do not support prediction 3: male chimpanzees did not raise the stakes following periods of absence.

Context 3: Social instability

We recorded 18hrs 10min of grooming across 254 bouts during the 'unstable period', consisting of 773 episodes, with a dyadic mean of 7.06 bouts (± SD = 7.28; median = 6.50) and 21.47 episodes (± SD = 27.22; median = 11.50). In this 'unstable period', males appeared to change their grooming behaviour when compared to the previous 'stable period'. Grooming bouts were significantly shorter (median bout length: 'stable period' = 290s; 'unstable period' = 186s; Wilcoxon signed-test: $Z = -2.072$, $N = 35$, $P = 0.038$) also showing a strong trend towards shorter episodes (median episode length: 'stable' = 96s, 'unstable' = 65s: $Z = -1.955$, $N = 9$, $P = 0.051$). Median rates of both episodes ('stable'= 2.41/hr; 'unstable'= 5.39/hr: $Z = -2.028$, $N = 7$, $P = 0.043$) and bouts ('stable'= 0.88/hr; 'unstable' = 2/hr: $Z = -2.197$, $N = 7$, $P = 0.028$) increased significantly, while the number of episodes per bout

393 significantly decreased (median 'stable' = 3.16 episodes/bout, 'unstable'= 2.32
394 episodes/bout: $Z = -2.547$, $N = 9$, $P = 0.011$). Overall, these results show that during
395 the unstable period, males engaged in shorter but more frequent grooming bouts,
396 which contained fewer and shorter grooming episodes.
397
398 Mean length of grooming episodes increased across bouts in the period of
399 social instability, with individuals significantly increasing episode duration over time
400 in more than half of the dyads (weighted Z-test: average: $r_s = + 0.063$, $P < 0.001$;
401 Table 2). Additionally, the amount of grooming individuals received during a bout
402 significantly matched the amount of grooming they gave their partner in the following
403 bout (LMM: *Estimate* ± *SE* = 0.22 ± 0.10, *Wald* = 4.590, $P = 0.035$). Only 23 bouts,
404 which correspond to 9% of the total number of bouts collected during social
405 instability, incorporated more than two intra-bout episodes. Within those bouts,
406 individuals did not significantly increase grooming episode duration in relation to
407 their own previous contribution (weighted Stouffer's Z-method: $N = 2$, $P = 1$; Table
408 6). Similarly, the number of bouts in which individuals did not increase episode
409 duration in response to partner's previous contribution significantly exceeded the
410 number of bouts in which episode duration increased throughout the bout (weighted
411 Stouffer's Z-method: $N = 2$, $P < 0.001$; Table 6). These results indicate that *M-group*
412 males during social instability raised the stakes across bouts by increasing episode
413 length across subsequent grooming interactions and matching partner's grooming
414 investment in the previous bout, which supports prediction 4, although they did not
415 raise the stakes within bout.
416 While rates of aggression were higher in the 'unstable period' than in the
417 'stable period' (Kaburu et al., 2013), these tended to decrease across the period,

418 although the relationship did not reach significance ($r_s = -0.316$, $N = 32$, $P = 0.078$).
419 Finally, daily variation in episode length was not significantly predicted by aggression
420 rates (LMM: *Estimate* ± *SE* = 0.31 ± 0.30, *Wald* = 1.097, *P* = 0.299).
421

422 **Discussion**

423

424 We found no support for raise-the-stakes as a grooming-allocation strategy
425 among wild male chimpanzees during periods of social stability (supporting our
426 *prediction 1*), a result consistent with studies on monkeys (*Papio cynocephalus*:
427 Barrett et al. 2000; *Macaca radiata* & *Cebus capuchinus*: Manson et al 2004;
428 *Cercocebus atys* & *Chlorocebus aethiops*: Fruteau et al. 2011). Male chimpanzees
429 might not raise the stakes not only because of the long history of social interactions
430 that characterize group members, but also because of the time limits that constrain
431 them. In other words, as during a day individuals have to engage in a broad range of
432 activities, including grooming more than one partner (Henzi et al. 1997; Dunbar,
433 1992), increasing grooming time with a partner might not always be a viable strategy
434 (Barrett et al. 2000). Contrary to our *predictions 2* and *3*, male chimpanzees did not
435 use the strategy in either post-conflict situations or after prolonged absence. However,
436 we did find support for raise-the-stakes during social instability, supporting our
437 *prediction 4*: in this context, individuals matched partner's contribution from the
438 previous bout and showed a general tendency to increase their grooming investment
439 across bouts, which was not a by-product of the decrease of aggression rates across
440 the unstable period. .
441

These findings suggest that RTS might be a viable strategy not only while cooperating with strangers but also in periods of social instability when relationships – prior histories of interaction – between the individuals become unreliable. Such instability may create conditions of uncertainty and unpredictability, comparable to situations in which individuals have to cooperate with strangers.

Grooming is commonly viewed as a means to build trust (Seyfarth 1977, 1980; Dunbar 1988, 1991; Henzi et al. 2000; Watts, 2002) to create a platform (a relationship) upon which future cooperation and contingent fitness benefits can be based (Hinde, 1976). Under this 'valuable relationships' model (Kummer 1978; Cords and Aureli 2000), we can conclude that trust was not sufficiently disrupted by either long absences caused by consortships or routine acts of aggression to require a RTS strategy to rebuild a relationship. The analysis of post-conflict contexts reveals also that not only did male chimpanzees not increase their investment, but also that former opponents rarely engaged in grooming bouts after conflicts, which is consistent with previous studies on this community (Kutsukake and Castle, 2004). It is possible that given the social stability that characterized the majority of the study period, with low rates of male-male aggression (Kaburu et al., 2013), aggressive interactions and the shifting of social interactions between group members might have had a minimal negative impact on social relationships between former opponents or for consorting males, and, thus, males might have not needed to rebuild predictable cooperative relationships 'from scratch' after conflicts, or after a prolonged absence.Additionally, Male chimpanzees might have no need to employ a RTS strategy to rebuild trust or repair

466 relationships after conflict or long periods apart if grooming is traded for other
467 commodities and for itself (Newton-Fisher & Lee, 2011; Watts 2002; Mitani 2006;
468 Gomes and Boesch 2011), or if groomers receive immediate benefits by decreasing
469 their stress levels (Shutt et al. 2007) or feeding on the parasites removed (Tanaka and
470 Takenfushi, 1993; Onishi et al., 2013; Johnson et al., 2010). Male chimpanzees,
471 however, raised the stakes when there was an increase in social instability. The
472 unexpected and unusual coalitional killing of the alpha male appeared to have offered
473 a condition that led individuals to (re)-build predictable cooperative relationships: the
474 trust on which social relationships were built broke down and needed to be re-
475 established. Our study therefore provides the first evidence of raise-the-stakes in
476 primate social grooming, albeit restricting to a particular context.
477
478 The presence of a raise the stakes pattern across bouts, including
479 unidirectional grooming (see data analysis), and its simultaneous absence within bout
480 confirms that unidirectional grooming plays an important role in male strategies to
481 enforce grooming reciprocation. In contrast, studies on monkeys have generally
482 focused exclusively on grooming bouts in which both partners groomed (Barrett et al.
483 2000; Manson et al. 2004; Fruteau et al. 2011). While this makes sense for species
484 whose grooming bouts are predominantly reciprocated within bout, such as vervet
485 monkeys (*Chlorocebus aethiops*) and sooty mangabeys (*Cercocebus atys*) as 90% of
486 their grooming bouts were found to be reciprocated (Fruteau et al. 2011), this
487 approach is less understandable for species in which reciprocated bouts are less than
488 half of the total number of bouts, which is the case of, for instance, chacma baboons
489 (31-51%: Barrett et al. 1999), bonnet macaques (5-7%: Manson et al. 2004), and
490 white-faced capuchins (12-27%: Manson et al. 2004). The results presented in this

chapter indicate that unidirectional grooming should receive more consideration in future studies and its importance in the analysis of grooming interactions should not be discounted.

Since our analysis is based on an unusual social context (i.e. social instability due to the alpha male's death) and on a relatively small sample size (e.g. only two males were recorded spending a considerable amount of time far from the other group members) our results need to be taken with caution. Nevertheless, our study highlights the importance of considering the possibility that individuals adopt some strategies to enforce reciprocation and avoid cheating in specific contexts, rather than as a general approach. Given the complexity of chimpanzee social system and grooming patterning, it would not be plausible to suppose that male chimpanzees engage in a single strategy to assure reciprocation. In contrast, it is more likely that they change the strategies adopted in relation to, for instance, the stability of the hierarchy, rank relationships, or the presence of bystanders. Therefore, future work might attempt to test for the RTS strategy in specific social contexts in which a re-establishment of predictable cooperative relationships is needed, such as during social instability among male baboons following the immigration of new males (Wittig et al. 2008; Beehner et al. 2005), or in chimpanzee communities, such as *Kanyawara* (Kibale, Uganda) that exhibit higher rates of aggressive interactions (Muller 2002; *cfr.* Kaburu et al., 2013), or that show higher levels of post-conflict grooming (e.g. *Ngogo*: Watts, 2006). This might potentially shed light on whether partners that can no longer rely on their prior history of interactions resort to a RTS strategy to re-establish cooperative relationships.

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Table 1. Number of focal observation hours on each of 8 adult male chimpanzees.

Focal Individuals	Focal Observation Time
AL	49hr 45min
BB	54hr 53min
CT	48hr 54min
DE	53hr 11min
FN	46hr 01min
OR	47hr 03min
PM*	40hr 14min
PR	57hr 15min

**PM* was killed on the 2nd of October 2011 (Kaburu et al. 2013).

Table 2. Spearman rank correlation between length and order of occurrence of grooming episodes. The grooming contribution of each male to each of the grooming dyad he was part of was tested individually and the results were combined through weighted Z-test. Only males that performed at least 5 grooming episodes were included in the analysis. The table shows 1) the context from which grooming data were extracted, 2) the range of p values, 3) the range of coefficients of Spearman's correlations (r_s) and 4) the percentage of individuals showing a positive trend (grooming episodes increased over time) and a negative trend (grooming episodes decreased). RTS in post-conflict context was analysed exclusively within-bout (Table 4).

Context	**N**	**p range**	**r_s range**	**% r_s (+)**	**% r_s (-)**
Social stability	71	$0.00<p<0.934$	$-1<r_s<0.835$	35 %	65%
After prolonged absence	25	$0.019<p<0.466$	$-0.9<r_s<0.6$	40%	60%
Social instability	39	$0.01<p<0.497$	$-0.80<r_s<0.771$	57%	43%

Table 3. Sign tests to assess whether groomers increase episode duration in response to their own previous contribution or to partner's during social stability (February-September 2011). The test was run only when at least five dyads contributed to a group, but we included also groups for which the test was not run to show the trend.

	Increase across bouts								
	in response to their own previous contribution						**in response to partner's previous contribution**		
	Initiator			**Reciprocator**					
N	**Yes**	**No**	**Sign test *P***	**Yes**	**No**	**Sign test *P***			**Sign test *P***
3	15	20	0.5	-	-	-	5	30	<0.000
4	6	4	0.754	5	5	1	1	9	0.021
5	1	3	-	3	1	-	1	3	-
6	0	3	-	0	3	-	0	3	-
7	0	1	-	1	0	-	0	2	-
23	0	1	-	0	1	-	0	1	-

N = number of intra-bout episodes.

Table 4. Sign tests to assess whether groomers increase episode duration in response to their own previous contribution or to partner's in post-conflict context. The test was run only when at least five dyads contributed to a group, but we included also groups for which the test was not run to show the trend.

	Increase across bout								
	in response to their own previous contribution						**in response partner's previous contribution**		
	Initiator			**Reciprocator**					
N	**Yes**	**No**	**Sign test *P***	**Yes**	**No**	**Sign test *P***	**Yes**	**No**	**Sign test *P***
	2	5	0.453				1	6	0.125
4	1	1	-	0	2	-	0	2	-
7	0	1	-	0	1	-	0	1	-
21	0	1	-	0	1	-	0	1	-

N = number of intra-bout episodes.

Table 5. Sign tests to assess whether groomers increase episode duration in response to their own previous contribution or to partner's after a prolonged absence due to consortship. The test was run only when at least five dyads contributed to a group, but we included also groups for which the test was not run to show the trend.

	Increase across bout								
	in response to their own previous contribution						**in response to partner's previous contribution**		
	Initiator			**Reciprocator**					
N	**Yes**	**No**	**Sign test *P***	**Yes**	**No**	**Sign test *P***	**Yes**	**No**	**Sign test *P***
3	1	4	0.375				0	5	0.063
4	2	0	-	0	2	-	0	2	-
7	0	1	-	0	1	-	0	1	-

N = number of intra-bout episodes.

Table 6. Sign tests to assess whether groomers increase episode duration in response to their own previous contribution or to partner's during social instability. The test was run only when at least five dyads contributed to a group, but we included also groups for which the test was not run to show the trend.

	Increase across bout								
	in response to their own previous contribution						in response to partner's previous contribution		
	Initiator			Reciprocator					
N	**Yes**	**No**	**Sign test *P***	**Yes**	**No**	**Sign test *P***	**Yes**	**No**	**Sign test *P***
3	7	6	1				0	13	< 0.001
4	3	2	1	3	2	1	0	5	0.06
5	0	2	-	0	2	-	0	2	-
6	0	1	-	0	1	-	0	1	-
7	0	2	-	0	2	-	0	2	-

N = number of intra-bout episodes.